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Review of Factors Affecting Fecundity, Oviposition, and Egg Survival of Grasshoppers In North America

ABSTRACT

The reproductive potential among adult grasshoppers of one
season is the most important factor governing the potential
relative population of the subsequent season. Numerous biotic
and abiotic factors affect the number and potential viability of
eggs for a given generation. Additionally, most grasshopper
species in North America spend about 10 months in the egg stage,
during which eggs are vulnerable to further depredation.
This review summarizes published research on factors affecting
production and survival of the egg stage, including weather,
nutritional status of parents, soil characteristics, parasites,
predators, pathogens, and other biotic and abiotic causes. It
is intended to increase understanding of what affects densities
of grasshopper hatchlings.

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REVIEW OF FACTORS AFFECTING FECUNDITY, OVIPOSITION, AND EGG SURVIVAL OF GRASSHOPPERS IN NORTH AMERICA

By George B. Hewitt[1]

Grasshoppers are one of the principal invertebrates on rangeland in North America. About 600 species occur within the United States, but only about 24 attain high densities and are considered major pests (Hewitt 1977). All 262 million hectares of rangeland in the United States are the habitat for some grasshopper species. About 99 percent of these species lay eggs during July-September and hatching takes place during April-June. Environmental, biotic, and population factors influence the number and survival of grasshopper eggs. Chapman et al. (1979) reported that the "loss of reproductive potential in the adult population in one year is the largest single factor affecting the size of the adult breeding population in the following year." However, the density of grasshoppers that hatch in the spring also is related directly to the egg-laying opportunities of adult females during the previous summer and to survival of eggs from the time of oviposition until hatching occurs.

Many workers have reported on different aspects of grasshopper biology and ecology, and some have contributed important reviews on such subjects as parasites and predators (Rees 1973), forage losses (Hewitt 1977), population biology (Hilbert and Logan 1981), and control (Hewitt and Onsager 1983). The critical factors that determine densities of grasshopper hatchlings are reviewed in this report. Included are references to most of the important papers on North American grasshoppers, with some reports on locusts that also apply to the grasshopper situation on rangeland in North America. The information on fecundity of important species, on environmental limitations imposed on the adults during oviposition, and on egg survival from oviposition to hatching should contribute to more accurate forecasts of spring densities.

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Weather

Grasshopper and locust densities fluctuate periodically throughout the world. These density changes have often been linked to the climate, mainly temperature. In North America, an area with wide extremes in diurnal and annual temperatures, grasshopper outbreaks have often occurred during hot, dry weather (Putnam 1954). The effect of temperature on egg production was first reported by Parker (1930). He reared field-collected Melanoplus sanguinipes (Fab.) and Camnula pellucida (Scudder) at constant temperatures of 22°, 27°, and 37°C. Results indicated that temperatures between 27° and 37° were favorable for egg production by M. sanguinipes, but C. pellucida had a range of only 32° to 37°. Parker (1930) realized that the potential for increase is largely determined by the number of eggs deposited and is primarily dependent on the number of hours during the egg-laying period when the air temperature is above 21°.

Drake et al. (1945) found that the first egg pods laid in the season are the largest and contain the greatest number of eggs. The average number of Melanoplus bivittatus (Say) eggs per pod decreased from 78.6 in the first week of oviposition to 44.8 in the seventh week in indoor cages and from 74.9 in the first week to 62.1 in the seventh week in outdoor cages. Pickford (1960) reported the rates of oviposition by M. sanguinipes were two or three times greater from maturation to September 18 than from September 18 to the end of the experiment. The number of eggs laid per female per day by grasshoppers during the different periods was as follows:

              June 20-Aug. 11 . . . . 6.12
              Aug. 11-29 . . . . 4.52
              Aug. 29-Sept. 18 . . . . 4.26
              Sept. 18-Oct. 1 . . . . 1.85
              Oct. 1-27 43

Pickford (1960) reported that the decline in fecundity as the season advanced was not a result of aging of the females but was attributed to a seasonal decline in temperature. The oviposition rate rose sharply when grasshoppers were brought from the field into the laboratory, where temperatures were higher. Again, Pickford (1962) reported that grasshoppers reared on similar foods in the laboratory laid up to three times as many eggs as those in the field because of higher temperatures in laboratory cages. He (1966a) also stated that spring weather can directly affect egg-laying patterns from year to year through its effects on nymphal developmental rates and consequently on the maturation of adults. Warm spring weather permits early grasshopper maturity and egg laying, whereas a cool spring may reduce egg deposition, especially if temperatures decline early in the fall. Pickford (1966a) also

reported that the rate of egg deposition was dependent largely on prevailing temperatures. When maximum temperatures averaged 26°C or higher during the fortnight, oviposition usually averaged four eggs per day per female or higher (about one egg pod per female every 4-5 days), but when temperatures averaged less than 16°, oviposition declined by more that 50 percent. Some egg pods were laid during cool weather when the average air temperature was only 6°-15°, provided the soil surface temperature exceeded 21° for short periods of time.

A progressive decline in fecundity as dates of hatching became later was reported by Pickford (1960). In one study (Pickford 1966a), egg production decreased in 2 out of 3 years as hatching took place later in the season. It dropped from 11.0 to 5.4 pods per female in 1961 and from 7.5 to 4.8 pods per female in 1962, probably due to lower temperatures. Generally, as grasshoppers hatched later in the season and consequently reached the adult stage later, they laid pods with larger numbers of eggs. Eggs per pod averaged 20.91 in June, 21.80 in July, and 23.51 in August, but such slight increases could not compensate for reductions in numbers of pods.

Visscher et al. (1979) reported on the effect of insect rearing temperature and environment temperature of the host plant on fecundity and egg viability of the grasshopper Aulocara elliotti (Thomas). In general, both fecundity and egg viability of A. elliotti were reduced by cool rearing temperatures. However, the growing temperature of the host plant, western wheatgrass, significantly affected grasshopper fecundity, egg viability, and female longevity. The rate of reproduction in two populations was greatest when females were fed grass grown in a cool environment (18°-24°C). Also, two field populations reared in the laboratory differed in their ability to lay viable eggs at cool temperatures.

Apparently for maximum egg production, grasshoppers must mature early in the season to take advantage of optimum egg-laying periods during the summer. Early maturation is dependent on warm temperatures in the fall to allow for maximum embryo development and on high temperatures in the spring for early hatching and development.

Adult grasshoppers are seldom affected by midsummer weather extremes. For example, Spencer (1940) reported that all observed nymph and adult grasshoppers survived hailstorms in the summers of 1930 and 1939, even though hail accumulated to depths of 24-75 mm. However, killing frosts in September and October frequently terminated their populations.

Food Plants   Even though hot, dry weather is the most favorable for
grasshopper growth and development, a severe drought can reduce
plant growth and grasshoppers may starve (Parker 1939). If they
survive extended drought periods, fecundity is usually reduced
because of decreased food quality and quantity (Parker 1939,
Scharff 1961, Pickford 1963). Tauber et al. (1944) fed drying
food such as corn, alfalfa, and timothy to caged M. bivittatus
and reported egg production in proportion to each plant's
resistance to drying out. Thick cornstalks retained the most
moisture, and females feeding on this plant laid the most eggs.
Andrewartha (1944) reported that the threshold for increase of
the Australian grasshopper Austroicetes cruciata Saussure is
never reached because the food supply dries up and the
grasshoppers die from starvation before laying their full
potential of eggs. Late spring or early summer rain that
prolongs plant growth is the most important factor influencing
fecundity of this species. In Nigeria, low food quality caused
by low rainfall also resulted in a low number of eggs per pod
and delayed oviposition in the grasshopper Zonocerus variegatus
(L.) (Chapman et al. 1979). During periods of drought, a lack
of plant moisture may result in increased cannibalism. Tauber
et al. (1944) fed M. bivittatus dry food alone or with water.
Cannibalism was very pronounced in cages without water, but none
occurred in cages with water.

Some workers (Smith et al. 1952, Pickford 1958) have reported
differences in fecundity when using different food plants.
Tauber et al. (1944) said that wild lettuce, alfalfa, red
clover, garden lettuce, or onion plant fed as separate foods
resulted in better egg production than a mixed diet for
M. bivittatus. However, other researchers found that females
laid more eggs when fed a mixed diet (Barnes 1955, Pickford
1962).

Pfadt (1949) found that M. sanguinipes fed dandelion produced
3.48 egg pods per female during the first 3 weeks of the
oviposition period compared with 0.27 for females fed native
grasses and sedge. In fact, grasses have been an unfavorable
food plant for both C. pellucida and M. sanguinipes (Putnam
1962, Pickford 1962, 1963). Grasshoppers reared on grasses laid
fewer eggs. Pickford (1963) suggested that the dominant grasses
of the prairie region contributed little or nothing to the
reproductive capacity of C. pellucida but merely provided a
suitable breeding site. Alfalfa also adversely affected
fecundity when fed exclusively to several species of Melanoplus
(Brett 1947, Pfadt 1949, Barnes 1955, 1963, Bailey and Mukerji
1976, Hewitt et al. 1982). Barnes (1959) and Mulkern et al.
(1962) noted that grasshopper populations were higher in weedy
alfalfa fields than in weed-free fields and indicated that a
mixed diet is beneficial for population buildup of some

grasshopper species. Smith and Northcott (1951) fed
M. sanguinipes wheat grown in nutrient solutions of varying
nitrogen content and reported that females fed on wheat with a
high nitrogen content laid more eggs. In a followup study,
Smith (1960) varied the phosphorus content of wheat and found
that M. sanguinipes developed fastest, lived longest, and laid
the most eggs on wheat with a low phosphorus content.

**Soil
Characteristics**

Most grasshoppers and locusts select certain soil types for
oviposition. Studies on Locusta migratoria migratorioides
(Reiche and Fairmaire) showed that this locust preferred moist
compact sand for oviposition (Kennedy 1949, Choudhuri 1956).
Sand color and particle size apparently did not influence
ovipositional preference, but temperature of the sand surface
had a marked effect. Most pods were laid at 36°-38°C (Choudhuri
1956, Popov 1959). Woodrow (1965) reported that Locusta females
were able to detect inorganic salts and hydrochloric acid in
medium provided for oviposition, and they would reject the
oviposition site if the concentration was too high.
Schistocerca gregaria (Forskål) apparently prefers moist sands
and silts (Popov 1954). Hunter-Jones (1964) incubated egg pods
and individual eggs of S. gregaria in a series of sand-water
mixtures at a constant temperature of 28°. He found that most
eggs incubated in water-logged sand and that no eggs hatched in
sand containing only 0.6 cm^3 of water to 100 g of sand. In
all intermediate mixtures, the percentage of eggs that hatched
was independent of the amount of water present. However, Norris
(1968) reported that S. gregaria discriminated less at very high
water content, and many pods were laid in saturated sand
provided no water was on the surface. He also said that digging
by female grasshoppers was stimulated by sand that was dry on
the surface; if the dry layer did not exceed 4 cm, more pods
were laid than in sand that was moist throughout. Ovipositional
preferences for two British grasshoppers were studied by
Choudhuri (1958). Chorthippus parallelus (Zetterstedt)
preferred moist, medium to fine, loose sand and Chorthippus
brunneus (Thunberg) preferred dry, coarse, compacted sand.

Grasshoppers in North America also show differing preferences
for a wide range of oviposition sites. Edwards and Epp (1965)
found that M. sanguinipes females preferred moist sand to all
other oviposition sites and avoided completely dry soil. The
increased time spent probing in dry sand resulted in a decrease
in successful oviposition. Females would probe and dig at
random but would not deposit eggs if the subsurface soil was
dry. Soil water pH had little influence when egg pods were laid
in soils with a pH ranging from 3.0 to 11.6. However,
C. pellucida laid eggs in loose dry soil, a type of oviposition
habitat that was highly unpreferred by M. sanguinipes (Pickford
1974). Over a period of 15 days, C. pellucida females laid 112
egg pods in dry sand compared with 36 in moist sand.

Parasites

Insect parasites of grasshoppers include members of the families
Anthomyiidae, Nemestrinidae, Sarcophagidae, and Tachinidae of
the order Diptera. The Sphecidae (Hymenoptera) and several
species of mites, nematodes, and horsehair worms also attack
grasshoppers, but dipterous parasites are probably more
widespread and have greater effect on adult grasshopper numbers.

Percent parasitism usually increases throughout the summer in
the northern prairie region and is highest in September (Smith
1964). Most grasshoppers are killed by mature parasitic larvae
when they emerge from the host. According to Smith (1964), the
criteria for assessing the importance of a parasite in
population dynamics are the variations in its percent abundance
from year to year and the level of mortality at which it
operates. Both York (1955) and Lavigne and Pfadt (1966)
reported that the parasitization of female grasshoppers was much
higher than that of males. Although the literature on
grasshopper parasites is extensive (Rees 1973), data necessary
to quantify the effect of parasites on grasshopper populations
are not generally available.

Prescott (1960) studied egg production and mortality of
parasitized Melanoplus femurrubrum (De Geer), M. sanguinipes,
and M. bivittatus. He found that parasitism by the nemestrinid
Neorhynchocephalus sackenii (Williston) markedly reduced both
adult longevity and egg production. Field observations have
shown that outbreak grasshopper populations have been
drastically reduced by nemestrinid parasites (York and Prescott
1952, and Prescott 1960). However, Lavigne and Pfadt (1966)
indicated that parasites had a minor role in regulating Wyoming
grasshopper populations. Low rates of parasitism do not
necessarily indicate the inability to control populations, since
they must be considered in relation to all other causes of
mortality. Some grasshopper species appear to be more
vulnerable or susceptible to parasitism than others. However,
Huggans and Blickenstaff (1966) found that relative parasitism
among species tended to change during the season according to
the relative abundance of potential hosts.

Invertebrate Predators

There are about 1,451 species of North American Asilidae
representing 85 genera, some of which destroy grasshoppers
(Martin 1965). On open Wyoming rangeland, three species of the
genus Stenopogon prey primarily on grasshoppers, whereas nine
other species use grasshoppers only to supplement their diet
(Lavigne and Pfadt 1966). These authors estimated that if a
given area was occupied by Stenopogon spp. during the entire

summer, a robber fly could eat 6 grasshoppers per day or 540 in 90 days. They determined the robber fly and grasshopper density at a site in Wyoming and then estimated that grasshopper mortality due to robber flies ranged between 11 and 15 percent. The actual effectiveness of asilids therefore depends on the density of both asilids and grasshoppers. However, Rees and Onsager (1982, 1984) reported that asilid flies of the genera Efferia and Mallophorina also feed on grasshopper parasites, reduce the effectiveness of the parasites, and thereby enhance the survival of grasshoppers.

Wasps of the family Sphecidae also are efficient grasshopper predators, as the females provision their nests with Orthoptera. Lavigne and Pfadt (1966) reported that one wasp could use eight grasshoppers per day. They suggested that since these wasps are relatively rare, they may have only a minor role in grasshopper control. However, Newton (1956) pointed out that three species of the genus Tachysphex in Idaho reduced populations of "20-30 Oedaleonatus enigma (Scudder) per square yd to one in five square yds."

Ants have also been reported capturing early instar grasshoppers (Riley 1878, Greathead 1963). Observations by Lavigne and Pfadt (1966) showed that in one instance ants brought in one first instar nymph to their nest every minute and on another occasion one every 4 minutes. However, predation is limited to first instar nymphs as they emerge from egg pods. Mantids (Mantidae) have also been reported as predators of grasshoppers, but very few observations of predation have been recorded (Greathead 1963, Lavigne and Pfadt 1966).

Spiders (Araneida) prey on rangeland grasshoppers. In one study, Greathead (1966) reported spiders killed 4 percent of first and second instars of the desert locust. Lavigne and Pfadt (1966) pointed out that some spiders spin webs and capture grasshoppers, whereas others capture prey on the ground. They reported that the spider Schizocosa minnesotensis Gertsch consumed one nymphal grasshopper a day in cages, but the number consumed in nature is difficult to determine because the feeding habits of rangeland spiders are relatively unknown.

Mites (Trombidiidae) are commonly observed on the wings or thorax of grasshoppers. Lavigne and Pfadt (1966) reported that of 35 Wyoming grasshopper species examined, 21 were infested with mites. The number of mites per individual grasshopper ranged from 1 to 41, with 1 or 2 per individual being most common. They could not determine whether the mites were detrimental to the health of the grasshoppers, but Drake and Decker (1932) and Harper (1952) thought that mites on females probably reduced egg production.

Terrestrial Vertebrates

Several species of mammals, reptiles, and amphibians have been recorded as feeding on grasshoppers (Harper 1952, Wakeland 1958, Lavigne and Pfadt 1966). Skunks and coyotes frequently consume nymphs and adults, whereas badgers, bobcats, and foxes do so occasionally (Wakeland 1958). Toads, snakes, lizards, and frogs have also been recorded as grasshopper predators (Drake and Decker 1932, Harper 1952, Lavigne and Pfadt 1966). For example, five of six species of lizards studied in Wyoming consumed grasshoppers (Lavigne and Pfadt 1966). Rodents also utilize grasshoppers as food (Wakeland 1958). Lavigne and Pfadt (1966) reported that populations of the northern grasshopper mouse, Onychomys leucogaster arcticeps Rhoads, peaked with grasshopper populations. When grasshoppers were controlled, mouse populations also declined, very likely owing to lack of available food.

Birds

References to birds feeding on grasshoppers are too numerous to list. The effect of bird predators, however, is difficult to determine. Bird predation on the desert locust is erratic and dependent on habitat, season, and locality (Greathead 1966). Ashall and Ellis (1962) showed that birds can be effective in controlling only small gregarious locust populations. Stower and Greathead (1969) reported that birds reduced a nongregarious locust population by 4 percent.

Three species of birds common to the North American prairie that feed on grasshoppers are the horned lark, Eremophila alpestris (L.), the western meadowlark, Sturnella neglecta Audubon, and the lark bunting, Calamospiza melanocorys Stejneger. Lavigne and Pfadt (1966) estimated that a flock of 200 nesting lark buntings ate at least 84,000 grasshoppers in a 60-day period. Shotwell (1930) claimed the lark bunting was the most important bird predator of grasshoppers in Montana. A study in California by Bryant (1912) showed that birds were destroying more than 120,000 grasshoppers daily per square mile.

Pathogens

The common pathogenic micro-organisms in grasshoppers under natural conditions include bacteria, fungi, viruses, and protozoa. Their impact on grasshopper populations has not been precisely documented. However, the fungus disease Entomophthora grylli Fresenius has been reported as causing high grasshopper mortality over large areas of the northern Great Plains (Henry and Onsager 1982) and in Nigeria (Chapman et al. 1979). In 1977, widespread infections reduced grasshopper numbers at a

site in Montana from 25 per square meter on May 23 to less than 0.5 per square meter by mid-August (Hewitt 1979). Riegert (1967b) reported that this pathogen was very common during periods of high populations of C. pellucida in Canada and was one of the most effective natural measures of control. This fungus has also been reported in the grasshopper Z. variegatus in Nigeria, where high grasshopper mortality was associated with high rainfall (Chapman et al. 1979). Most attempts to control grasshoppers and locusts with either fungi or bacteria had little or no effect on grasshopper densities because these organisms require specific conditions for the initiation of infections (Henry 1970).

The protozoan Nosema locustae Canning has been studied extensively (Henry 1972, Henry and Oma 1981). Henry (1972) examined 31,570 grasshoppers collected in Idaho over a 5-year period and reported 5.05 percent were infected with N. locustae. The incidence of infection was highest (8.11 percent) in 1966 and lowest (1.60 percent) in 1967. Laboratory studies showed that egg production of Melanoplus differentialis (Thomas) decreased with increasing infection rates and spore concentrations (Henry and Oma 1981). They also reported that infections in males reduced fecundity, probably because males failed to inseminate the uninfected females or because their sperm failed and the females reabsorbed the eggs. However, the effect of infections on egg production under natural conditions is unknown. Viruses also have been isolated from grasshoppers, but their effect on grasshopper fecundity has not been determined.

Crowding

A common response of insects to crowding is a decrease in reproductive rates. The effects of crowding on Acrididae were first studied in relation to the solitaria and gregaria phases of Locusta spp. and Schistocerca spp. locusts. Norris (1950) compared reproductive rates between gregaria and solitaria adults of the African migratory locust when reared in isolation and under crowded conditions. She reported the average fecundity (total number of eggs laid) of crowded solitaria females was 497 and that of crowded gregaria was 330. The average clutch size of both phases in isolation was 71. Crowding reduced clutch size to 59 in gregaria but not in solitaria. The author concluded that the fecundity and rate of sexual maturation of both solitaria and gregaria held in isolated pairs as adults were greater than for gregaria held under crowded conditions. It is implied that the detrimental effects of crowding result from interference with feeding activities. Norris (1952) also showed that the effect of density on sexual maturation in Schistocerca is the opposite of its effect on Locusta, in which the solitaria and isolated gregaria mature much more rapidly than the crowded gregaria.

Locusta solitaria females mature in an average of 10.6 days and lay an average of five pods in the first 4 weeks, a much higher rate than for *Schistocerca* at any density.

The effects of crowding on some Acrididae have been summarized by Dempster (1963). He reported that increases in population density decrease fecundity in the three most studied genera—*Locusta*, *Schistocerca*, and *Nomadacris*. Crowding was also shown to stimulate ovipositing females of *S. gregaria* to lay eggs in close groups (Norris 1963). When grasshopper decoys were grouped, the majority of females oviposited near the decoys instead of a nearby site without decoys. The tendency to oviposit in a group could override a preference for oviposition in moist soil.

In only a few studies have North American "solitary" grasshoppers been examined, and these have been limited primarily to *M. sanguinipes*. Riegert (1965) reared adult *M. sanguinipes* in the laboratory as groups of pairs, as groups in association with mature and immature males, as single pairs, and as groups of unmated females. He reported that females of grouped pairs produced a larger number of eggs per pod and laid more viable eggs than those of other groupings. Peak egg production was reached sooner by females of grouped pairs (4 weeks) than by unmated females (7 weeks). Smith (1969) also reported fewer eggs per pod from virgin females than from crowded mated females, resulting possibly from slower mobilization of egg-producing materials. Virgin females required 8.3 days to produce a pod, whereas mated females required only slightly more than 2 days. In another study with *M. sanguinipes*, Smith (1970) reported that the number of pods and the number of eggs per female decreased as crowding increased. For example, each female produced an average of 605.8 eggs based on 1 pair per cage compared with an average of 359.6 eggs from 20 pairs per cage. Visscher (1971) also found fecundity to be inversely proportional to density in the grasshopper *A. elliotti*. The average number of progeny per female reared at 1 pair per cage was 44.8, whereas the number per female reared with 3 males per cage was 26. Some responses of crowding are therefore common to both grasshoppers and locusts.

Mating Activity

Parker (1930) was one of the first to theorize on why some grasshopper species consistently become abundant, whereas others seldom or never increase to outbreak numbers. He suggested less abundant species are limited in their capacity for increase because their ovaries produce only a small number of eggs, whereas abundant species have more specialized ovaries and egg production continues throughout the adult life as long as temperatures are favorable. Pickford et al. (1969) showed that a diffusible chemical substance from the accessory glands of

mature males stimulated virgin females of M. sanguinipes to oviposit. They implanted glands from mature males but reported that the effect was then weaker than produced by normal coupling.

The length of the mating period in relation to fecundity was studied by Pickford and Gillott (1976). They reported that females permitted an uninterrupted copulation every second week laid almost twice as many eggs as females allowed to couple for only 5, 10, 20, 30, or 40 minutes. The highest egg hatch (42.9 percent) was for females with uninterrupted copulation. Thus, if fertility is related to mating, cool, damp weather could possibly have a negative effect on mating and result in reduced fecundity. However, Smith (1968), working with M. sanguinipes, found no significant difference in fertile eggs produced between females that had copulated once and then were reared alone versus pairs of females and males reared together. Chapman et al. (1979) found differences in fecundity between short- and long-winged forms of Z. variegatus but did not speculate on the cause.

Sublethal Insecticides

Research has been limited on the effects of sublethal doses of pesticides on surviving grasshopper populations. Moriarity (1968) found no obvious effects of sublethal doses of two chlorinated hydrocarbons, DDT or dieldrin, on the grasshopper C. brunneus. MacCuaig and Watts (1965) conducted tests with aldrin and dieldrin on S. gregaria to determine whether fecundity was affected. They found the average number of egg pods laid per week per treated female equaled or surpassed numbers from control groups. The resulting eggs proved to be fully viable. However, Watts (1969) reported dieldrin could be translocated to the eggs of S. gregaria and could cause death in newly hatched nymphs. With increased interest in the organophosphates and carbamates, Kreasky and Mazuranich (1971) tested sublethal doses of naled, carbaryl, malathion, and the solvent acetone on the grasshopper M. sanguinipes. They reported the average eggs per female per day in the untreated control group was nearly double that of the treated group.

Temperature

Parker (1930) was one of the first researchers to study the effect of temperature extremes on grasshopper egg pods. He exposed eggs of M. sanguinipes and C. pellucida to low temperatures for 16 hours and concluded that overnight exposure to −25° to −30°C would kill 50-100 percent of the eggs. He also studied the effects of high temperatures on eggs of both species and concluded that eggs would be in danger if exposed 3 or more hours at 45° and would be killed by a 2-hour exposure at 50° or a 20-minute exposure at 60°. He pointed out that grasshopper eggs would probably not be killed by heat or cold when covered by soil to a depth of 5 cm, because temperatures would seldom be lethal. However, exposed eggs could be killed, because soil surface temperatures of 45° to 55° are common in many parts of the United States.

Clark (1947) measured soil and air temperatures in Australia and concluded that egg mortality occurs frequently in the oversummering eggs of the grasshopper A. cruciata during periods of high temperature (50°C). Dempster (1963) stated that egg mortality due to adverse weather is low in most years. Both Pickford (1966b) and Riegert (1967a) found that survival of grasshopper eggs during the winter in North America is dependent on snow cover and the intensity and duration of subzero air temperatures. Pickford (1966b) stated that temperatures lower than −26° for several days would result in high egg mortality. He pointed out that eggs usually withstand low soil temperatures, but during the winter of 1962-63, eggs stored in the soil outdoors at Saskatoon, Saskatchewan, suffered high mortality; from fall to spring, mortality ranged from 18 to 90 percent and averaged 70 percent. Pickford (1970) also stated that winter egg mortality is occasionally severe in Canada, especially when a protective snow cover is removed by a midwinter thaw and temperatures drop to a low level. He found that egg pods laid shortly before or during cool weather showed a marked increase in the percentage of nonviable or shriveled eggs. There may therefore be a short period during the first stages of egg development when the embryo is vulnerable to sharp drops in temperature. There is also evidence that some eggs laid late in the season enter winter in an undeveloped embryonic state and fail to hatch the following spring (Pickford 1966b).

Soil Moisture

Water is required for complete development of eggs of most Acrididae. Since most grasshopper species oviposit in damp soil, eggs usually receive sufficient moisture, but when drought conditions prevail, eggs may die from desiccation (Shotwell 1941, Birch and Andrewartha 1944, Dempster 1963, Riegert 1967b). Shotwell (1941) pointed out that species which lay eggs close to the surface, such as M. differentialis, suffer the most from drought. Birch and Andrewartha (1944) thought drought in Australia was the only factor that caused high mortality among

A. cruciata eggs in the field. A survey showed 54-75 percent
egg mortality at one location and 91 percent at another that was
due to summer drought. However, based on an analysis of
meteorological records in Australia, they estimated the
probability of high egg mortality due to drought at 12 times or
less per thousand years.

The susceptibility of eggs to desiccation varies with the
developmental stage of the embryo and is greatest for newly laid
eggs and least for diapause eggs (Birch and Andrewartha 1942).
The mortality rate of eggs in diapause was related to total
evaporation and to the duration of exposure to desiccation.
Pickford (1966b) reported that C. pellucida eggs laid early in
the season (July) of 1961 were severely affected by high
temperatures and very dry soil conditions. In more recent
studies, Mukerji and Gage (1978) examined the effects of soil
moisture on embryonic development and egg mortality of
M. sanguinipes. In a silty clay loam soil, a minimum soil
moisture of about 13.5 percent was necessary for eggs to
complete development and hatch without evidence of stress. A
model based on soil moisture and heat accounted for a maximum of
99 percent of the variance in hatching.

Excessive moisture has also been found to be detrimental to egg
survival. Parker (1930) submerged eggs and found mortality
proportional to duration of submergence. He concluded that even
if grasshopper egg pods were submerged for weeks, some would
still hatch. Clark (1947) reported a reduction in the number of
grasshoppers that hatched where excessive precipitation occurred
in Australia. However, he believed mortality was not a direct
result of flooding but rather was caused indirectly by
stimulation of fungi and bacteria. Dempster (1963) reported
that the extent of flooding is the most important factor
governing outbreaks of L. m. migratorioides. Spring floods can
cause high egg mortality if they occur after diapause has been
broken. Hogan (1965) reported on egg survival of Chortoicetes
terminifera (Walker) in Australia during periods of abundant
moisture. He submerged eggs at 17°C for 10 to 50 days and found
that survival ranged from 87 percent for eggs not submerged to
8 percent for eggs submerged for 50 days. Hunter-Jones (1964)
reported that restriction of oxygen in soils with high moisture
content was detrimental to the eggs. On North American
rangeland, however, prolonged submergence of eggs is very
unlikely.

Nymphs that hatch in very dry soil may be unable to exit the egg
pod. Both Parker (1939) and Shotwell (1941) observed nymphs
within hard-packed soil that were unable to make their way to
the surface. Nymphs may remain alive when trapped in an egg pod
for up to 6 days.

Maternal Effects

Little is known about the possible importance of maternal effects on the fluctuations of acridid populations. The growth rate of acridid embryos has been assumed to be determined by the genetic potential of the organism and is modified by the conditions of the environment. However, Visscher (1971) reported that embryonic growth rate of A. elliotti is largely determined by the mother, and conditions affecting the mother can affect embryonic development. Thus, environmental stresses that cause physiological changes in the adult generation could alter the rate and pattern of embryonic development in the progeny (Van Horn 1966a).

Van Horn (1966b) suggested that differences in growth of embryos from young versus old females and from crowded versus less crowded parents may be the result of differential incorporation of growth stimulating or inhibiting factors such as hormones into the yolk substrate. This conclusion is based on work that showed that the number of eggs laid per pod decreases with maternal age in A. elliotti, and that the rate of development of progeny from old females is greater than from young females.

Visscher (1971) also showed that populations of A. elliotti differed both in the fecundity of the parents and in the development rate of progeny reared under similar conditions. This perhaps explains why no consistent correlation has ever been reported between environmental influences and survival of populations of A. elliotti. Stresses imposed on the parental generation, plus the physiological capacity of the parental females to impart to the eggs factors essential for rapid growth of the progeny, are significant influences in the population dynamics of this species (Visscher 1971). However, Pickford (1963) found no significant differences in the percent hatch of eggs, nymphal survival, or weights of new F_1 adults when the parent generation of C. pellucida was fed different food plants.

Parasites and Predators

Of all insects that attack grasshopper egg pods, only the Scelionidae (Hymenoptera) are truly parasitic and develop within normal eggs. However, Chalcididae (Hymenoptera) egg parasites have been reported in grasshopper eggs when the eggs were laid in or on plant tissue instead of in the soil (Greathead 1963). Apparently Scelio sp. are of little importance in western Canada and Wyoming (Putnam 1953, Lavigne and Pfadt 1966), but parasitism may occasionally reach 25 to 40 percent in local areas. In northern areas of Canada, these parasites mature too late to have a major impact (Putnam 1953). Parasitism was reported ranging from 8 to 34 percent in California, but only in egg pods collected in irrigated fields (Harper 1952).

Insect families that prey on grasshopper eggs in North America include Bombyliidae (Diptera), Meloidae and Carabidae

(Coleoptera), and Gryllidae (Orthoptera) (Shotwell 1930, Parker 1939, Dempster 1963, Greathead 1963). Bombyliidae were reported as having the least effect (less than 2 percent predation) on grasshopper eggs in Wyoming (Lavigne and Pfadt 1966), but Parker and Wakeland (1957) reported 9.3 percent parasitism in 1938, 16.2 percent in 1939, and 10.3 percent in 1940. They also reported that Meloidae destroyed 3.7 percent of egg pods in 1938, 7.1 percent in 1939, and 8.5 percent in 1940. In Wyoming fall grasshopper egg surveys (Lavigne and Pfadt 1966), Meloidae destroyed an average of 13 percent of the egg pods at one location during an 8-year period and 8 percent at another location during a 5-year period. About 12 percent of the egg pods were destroyed by Carabidae larvae, which, along with the adults, are scavengers.

In East Africa, grasshopper egg predation by three insect species has been recorded as follows: Stomorhina lunata (Fab.) (Diptera) 7.5 to 46.2 percent, Systoechus somali Oldroyd (Diptera) 0.6 to 10.3 percent, and Trox procerus (Harold) (Coleoptera) 0.4 to 3.3 percent. Systoechus species also occur in North America. Crickets may occasionally prey on grasshopper eggs. Smith (1959) reported that in Canada the gut of the cricket Acheta assimilis luctuosus (Serville) contained eggs of M. bivittatus. Destruction of eggs was estimated at 50 percent in some localities.

An estimated 11 percent of the egg pods of Dissosteira longipennis (Thomas) were destroyed by several insect predators in Colorado in 1939 (Spain 1939). In general, grasshopper egg predation by insects in North America appears to be less than 50 percent at given sites, and probably averages less than 5-15 percent overall.

There are also numerous reports of animals such as ground squirrels, mice, skunks, birds, reptiles, and coyotes consuming grasshopper egg pods (Parker 1939, Telford 1943, Harper 1952, Wakeland 1958, Pickford 1965, and Riegert 1967a). Wakeland (1958) reported that birds and rodents destroyed 15 percent of the egg pods of D. longipennis at a site in New Mexico and 10 percent at a site in Texas. An estimate of egg pod destruction in Canada by ground squirrels was 48 percent in late autumn and a total of 90 percent prior to hatching in the spring (Pickford 1965).

Miscellaneous Factors

Grasshopper egg mortality also occurs from factors other than those mentioned previously. Popov (1959) reported that percent egg mortality of L. m. migratorioides due to desiccation, rot and mold, and nonviability was negligible as compared with mortality caused by natural enemies. Ashall and Ellis (1962) examined eggs of gregarious populations of the desert locust and

reported that just over 3 percent of apparently healthy eggs
failed to hatch. Nearly all pods contained a few shriveled
eggs, and the overall mortality varied between 0.9 and 18.7
percent. Mold was reported to cause egg mortality of up to 10
percent in different populations of locusts (Greathead 1963).
Egg mortality of the Australian plague locust, C. terminifera,
from factors other than parasitism ranged from 0 to 89 percent
(Hogan 1965). In North America, Riegert (1967b) reported egg
viability for three species of grasshoppers over a 21-year
period as follows: M. sanguinipes 80 percent, M. bivittatus 83
percent, and C. pellucida 84 percent.

Weather has a critical role in the rise and fall of grasshopper populations in North America through its effect on grasshoppers, food plants, and habitat. Temperature and precipitation are most important. Warm spring weather allows for faster development of the nymphs, earlier maturation of the adults, and thus an opportunity for oviposition when temperature conditions are most favorable. Warm weather during the time of egg laying also is important as egg deposition is reduced during cool weather.

Precipitation during late spring or early summer is necessary for production of quality grasshopper food. During periods of drought, grasshopper fecundity can be reduced by lack of food, reduction in plant quality, and an increase in cannibalism due to a lack of plant moisture. Most grasshopper species prefer moist sand for oviposition. However, some species such as C. pellucida prefer dry sand.

Climatic conditions vary widely from year to year in North America. Grasshopper populations may be near outbreak status or very low, depending on whether the weather is warm and dry, or cool and wet. Therefore, even though the prediction of grasshopper hatching density is possible, the actual fate of developing populations can be greatly modified by weather conditions acting on both nymphs and adults.

Biotic organisms affect nymphal and adult grasshopper populations in several ways. Organisms such as parasites, predators, animals, birds, and some pathogens often cause direct mortality. However, parasites and some pathogens may not kill the host immediately but may reduce both grasshopper longevity and fecundity. In general, the intensity of parasitism reported for grasshopper populations of several species has been 13 percent or less. The fungus disease E. grylli has drastically reduced grasshopper populations when environmental conditions have been favorable, but the overall effect of pathogens under natural field conditions is largely unknown.

High grasshopper mortality has been attributed to N. locustae, and infected grasshoppers usually have a decrease in fecundity; again, however, the actual degree of suppression by an epizootic is difficult to establish. Other factors that affect fecundity, such as crowding, mating, and environmental contaminants, are even more difficult to correlate with population fluctuations. Since such factors as crowding may affect different grasshopper species in different ways, the effects of density on fecundity are not predictable.

The inherent fecundity of individual species is important in determining the potential for increase. The temperature of the rearing environment and the quality of available food plants directly affect fecundity. One study indicated that stress on the adult generation affects embryonic development in the progeny, which in turn affects fecundity. Results of several field and laboratory studies on the fecundity of some of the more important species are shown in tables 1 and 2.

Egg density is probably the most critical indicator of the number of grasshoppers that will hatch in the spring; therefore, a greater understanding of factors affecting survival and viability should be of value in predicting spring densities. In general, egg mortality in North America due to temperature extremes is very low in most years. During the winter, when the egg pods are covered with soil and snow, soil temperatures never approach the lethal point. Likewise, high air temperatures are usually not lethal as long as the egg pod is covered with soil.

In North America, egg mortality may occur from general lack of soil moisture during extreme drought or when dry soil conditions prevail between oviposition and diapause. Excessive moisture may also be detrimental to egg survival, but submergence of eggs is unlikely in the Western United States. Soil moisture is therefore not critical for egg survival in most years in North America.

Probably the greatest source of egg mortality is from predators and parasites. For example, in northern North America, eggs remain in the ground for about 10 months and allow both insect and vertebrate predators time to decrease the hatching potential. There have been occasional reports of egg predation well over 50 percent, but in most studies, predation has been less than 15 percent. Eggs also fail to hatch from unknown reasons, but mold and disease organisms may be involved.

Assigning population reduction values to the many factors that affect fecundity and egg survival is difficult, because they vary from year to year and location to location. However, based on the overall review of such factors, one may speculate on their effect on a model population. The dominant factors affecting North American grasshopper populations between oogenesis in the summer until hatching in the spring are shown in figure 1.

All mortality values assigned the various factors are estimated, but they are reasonable averages based on studies of grasshopper populations.

During typical adult surveys, very little information is recorded pertaining to survival factors. However, if grasshopper density, species composition, and available food plants were recorded, the information in figure 1 could be used to predict spring densities.

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Table 1.--Grasshopper fecundity as determined by field studies

Reference	Food plants and/or rearing method	Av. number of pods/female	Av. number of eggs/female	Av. number of eggs/day (oviposition period)	Interval between egg pods (days)	Av. number of eggs/pod
			Camnula pellucida			
Drake et al. 1945	Mixed diet	1.9	129		10	70
Pickford 1966a, b	Mixed diet (3 yr field av.)	7.9	179		4-5	22.1
	Mixed diet (3 yr lab av.)		214			
	Mixed diet (June - field)					20.9
	Mixed diet (July - field)					21.8
	Mixed diet (Aug. - field)					23.5
	Mixed diet (Sept. - field)					25.5
			Melanoplus differentialis			
Drake et al. 1945	Mixed diet	1.4	128		14	88.8
			Melanoplus sanguinipes			
Drake et al. 1945	Mixed diet	6.0	117	3.7	4-5	19.6
Pfadt 1949	Dandelion	9.8	206	3.4		21.0
	Wheat	8.8	188	3.0		21.3
	Tansy mustard	7.5	160	3.2		21.4

Table 1.--Grasshopper fecundity as determined by field studies--Con.

Reference	Food plants and/or rearing method	Av. number of pods/female	Av. number of eggs/female	Av. number of eggs/day (oviposition period)	Interval between egg pods (days)	Av. number of eggs/pod
			Melanoplus sanguinipes (con.)			
	Alfalfa	7.6	157	2.4		20.7
	Thistle	3.9	71	1.7		18.4
	Kentucky bluegrass	3.5	65	1.9		18.6
	Bluestem	2.5	45	1.6		17.9
Smith et al. 1952	Wheat		117			
	Barley		86			
	Dandelion		65			
	Brome		53			
	Oats		50			
	Flax		46			
	Sweetclover		34			
	Alfalfa		13			
	Russian thistle		12			
Pickford 1960	Mixed diet	13.3		May 31, 1956 - Interior B.C.		23.8
		12.2		May 30, 1957 - Delisle, Sask.		21.9
		11.7		June 3, 1958 - Delisle, Sask.		
		9.4		June 3, 1958 - Lily Plain, Sask.		21.4

Pickford 1962	K-wheat + dandelion	209	3.7	22.3
	K-wheat	167	3.0	21.7
	Brome + dandelion	164	2.4	20.1
	K-wheat + R. thistle	138	2.2	18.5
	Dandelion	127	3.0	20.2
	Bromegrass	119	2.2	19.1
	Brome + R. thistle	97	1.9	17.7
	Russian thistle	22	.5	13.7

Table 2.--Grasshopper fecundity as determined by growth chamber, greenhouse, and laboratory studies

Reference	Rearing temp. (°C)	Food plants and/or rearing method	Av. number of pods/female	Av. number of eggs/female	Av. number of eggs/day (oviposition period)	Interval between egg pods (days)	Av. number of eggs/pod
		Aulocara elliotti					
Visscher et al. 1979	Warm environ.[1]	Field grass		37.3	0.71		
		Cool grass		51.1	1.04		
		Warm grass		23.4	.65		
	Cool environ.[1]	Field grass		9.0	.12		
		Cool grass		12.8	.24		
		Warm grass		9.5	.14		
	Warm environ.[2]	Field grass		35.5	.60		
		Cool grass		27.7	.64		
		Warm grass		25.0	.58		
	Cool environ.[2]	Field grass		10.0	.18		
		Cool grass		12.0	.20		
		Warm grass		7.0	.13		
Hewitt, G.B. (unpub. data 1983)							7.7

Parker 1930	37	Mixed diet	4.2				
	32		6.2				
	27		1.0				
	22		.2				
Shotwell 1941							10-38
			4				43-104
			2	127			
Smith 1966	30	Wheat + dried food mixture	8.2	355	11.0	3.9	43.3
Bailey and Mukerji 1976	30	Corn	4.0	196	7.1		50
		Lettuce	6.0	403	13.1		70
		Radish	6.3	450	14.9		74
		Mixed diet	5.7	412	13.1		75
Hewitt, G.B. (unpub. data 1983)	27	Mixed diet					43.0

Melanoplus differentialis

Sanderson 1939		Soybeans	2.6	305			112.0
		Wheat	1.8	209			115.9
		Cotton	1.0	73			73.0
Shotwell 1941				300			45-99
Hewitt, G.B. (unpub. data 1983)							106.5

See footnotes at end of table.

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Table 2.--Grasshopper fecundity as determined by growth chamber, greenhouse, and laboratory studies--Con.

Reference	Rearing temp. (°C)	Food plants and/or rearing method	Av. number of pods/female	Av. number of eggs/female	Av. number of eggs/day (oviposition period)	Interval between egg pods (days)	Av. number of eggs/pod
			Melanoplus femurrubrum				
Morton 1939				74			
Shotwell 1941							24-29
Bailey and Mukerji 1976	30	Corn	8.0	162	6.4		20.6
		Lettuce	12.0	302	9.7		25.5
		Radish	14.0	321	10.5		23.1
		Mixed	14.0	336	11.4		24.1
			Melanoplus packardii				
Shotwell 1941							17-29
Hewitt, G.B. (unpub. data 1983)	33		7.7			2.9	19.9
	27		4.8			5.3	19.6
			Melanoplus sanguinipes				
Parker 1930	24	Mixed diet	8.8			4-5	25
Morton 1939				144			
Smith and North-cott 1951		Wheat (high nitro.)		58			
		Wheat (low nitro.)		35			

Barnes 1955		Mixed diet	8.8	221			
		Hedgemustard	7.8	196			
		Johnson grass	4.1	89			
		Neetle-leaf goose foot	4.6	43			
		Alfalfa	1.0	13			
Pickford 1958, 1962	Night 21-24	Wheat and mustard	25.5	579	8.4		22.7
	Day 30-40	Wheat and flaxweed	23.1	467	7.9	2.6	20.2
		Lettuce and bran	21.6				20.2
		Mustard	20.5	431	6.6		21.0
		Dandelion	17.0	332	6.0		19.5
		Lettuce	14.4	298	5.0		19.3
		Russian pigweed	13.6	249	4.1		18.3
		Flaxweed	12.7	249	5.6		19.6
		Wheat	11.9	243	4.6		20.4
		Bromegrass	9.0	176	3.6		19.5
Smith 1960	30	Wheat (high phos.)	0				
		Wheat (low phos.)	1.2				

See footnotes at end of table.

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Table 2.--Grasshopper fecundity as determined by growth chamber, greenhouse, and laboratory studies--Con.

Reference	Rearing temp. (°C)	Food plants and/or rearing method	Av. number of pods/female	Av. number of eggs/female	Av. number of eggs/day (oviposition period)	Interval between egg pods (days)	Av. number of eggs/pod
		Melanoplus sanguinipes (con.)					
Riegert 1965	Night 24-27	Grouped (lettuce)	11.8	252	3.6	4.6	21.3
	Day 27-31	Prairie (lettuce)	10.6	180	3.0	3.3	17.0
		Unmated (lettuce)	7.6	139	1.4	8.7	18.2
Smith 1966	30	Wheat + dried food	15.1	329	9.4	2.3	21.8
Smith 1968	30	Single copulation	31.1	638	8.2		20.5
		Multiple copulation	26.1	539	9.3		20.7
Smith 1970	30	1 pair/cage (wheat + artificial diet)	26.0	606			22.1
		3 pair/cage	20.9	487			22.8
		10 pair/cage	20.6	484			22.5
		20 pair/cage	16.2	360			19.2
Pfadt et al. 1979	27-33	Mixed diet	10.3	229	6.7	3.6	22.4
Hewitt, G.B. (unpub. data 1983)	27	Mixed diet					17.4
		Phoetaliotes nebrascensis (Thomas)					
Shotwell 1941							18-20
Hewitt, G.B. (unpub. data 1983)							16.4

[1]Population collected at Decker, Mont.
[2]Population collected at Townsend, Mont.

Factors limiting oviposition	%
Weather	1
Food plants	3
Soil characteristics	1
Crowding	1
Mating activity	1
Biotic organisms	
Insect parasites	12
Invertebrate predators	20
Terrestrial vertebrates	4
Birds	12
Pathogens	5
	60

Adults

July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June

Eggs

Estimated population reduction

Density = $16/m^2$

  density = $8/m^2$

30% reduction of   during adult stage

5.6   lay 3 egg pods

2.4   lay 1 egg pod

Eggs laid = 336 + 48 = 384

50% reduction before hatching = 192

192 eggs/m^2 will hatch

Factors affecting egg survival	%
Temperature extremes	4
Soil moisture	1
Maternal effects	1
Parasites and predators	30
Miscellaneous factors (inviability, mold, hatching failure, etc.)	14
	50

Figure 1.--Factors affecting grasshopper numbers in North America during adult and egg stages.